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Larval brooding correlated with high early origination rates in cheilostome Bryozoa

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Article

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Abstract

Life-history traits such as dispersal affect population attributes like gene flow, which can have consequences for speciation and extinction rates over macroevolutionary timescales. Here we use the Cheilostomatida, a monophyletic order of marine bryozoans, to test whether a life-history trait, larval brooding, affected the origination and extinction rates of genera throughout their fossil record. Cheilostome lineages that brood their larvae have shorter larval dispersal distances than non-brooding lineages, which has led to the hypothesis that the evolution of larval brooding decreased gene flow, increased origination, and drove their Cretaceous diversification. Brooding cheilostomes are far more diverse than non-brooding cheilostomes today, but it remains to be shown that brooding lineages have a higher origination rate than non-brooders. We fit time-varying Pradel seniority capture–mark–recapture models to look at the effect of brooding on origination and extinction rates during the Cretaceous cheilostome diversification, the Cretaceous/Paleogene mass extinction and recovery, and through the Cenozoic. Our results support the hypothesis that brooding affects origination rate, but only in the Cenomanian to Campanian. Extinction rates do not differ between brooding and non-brooding genera, and there is no regime shift specific to the Cretaceous/Paleogene mass extinction. Our work illustrates the importance of using fossil occurrences and time-varying models, which can detect interval-specific diversification differentials.

Non-technical Summary

Larval brooding is a common parental care strategy with similar downstream effects on an organism's life cycle and ecology across marine invertebrate phyla. Organisms that brood their larvae generally produce larvae with less dispersal ability than unbrooded larvae. Lower dispersal in theory increases genetic differentiation between populations, which, all else being equal, is expected to increase the speciation rate of brooding lineages. In the Order Cheilostomatida of Bryozoa, a clade of marine, colonial, suspension-feeding invertebrates, larval brood chambers are often visible in fossil specimens. This allows us to infer which genera were brooding and non-brooding throughout the evolutionary history of cheilostomes. We use cheilostome bryozoans to test whether brooding cheilostomes have a higher genus-level origination rate than non-brooding cheilostomes. Brooding cheilostomes are far more diverse than non-brooding cheilostomes today, but alternatively, this may be because brooding cheilostomes have had a lower extinction rate than non-brooding cheilostomes. Our results support the hypothesis that brooding affects origination rate, but only during certain geologic intervals. Extinction rates do not differ between brooding and non-brooding genera.

Introduction

Rates of speciation and extinction in evolutionary clades depend in part on aspects of populations such as population size, gene flow, and geographic range (Stanley 1986; Jablonski and Roy 2003; Payne and Finnegan 2007). Life-history traits—traits involved in maturation and reproduction such as dispersal and fecundity—are major determinants of these population attributes (Stearns 1976; Emlet 1995). Certain life-history traits are correlated with more speciation (or origination at the genus level) or less extinction, so we might expect lineages with these traits to become dominant on macroevolutionary timescales (lineage sorting; Vrba and Eldredge 1984; Vrba and Gould 1986). Cases in the fossil record where we can observe life-history traits over macroevolutionary timescales are rare, but a few studies have demonstrated that life-history traits affect diversification rates across background and mass extinction intervals. In ostracods, species with greater sexual dimorphism had a higher extinction rate across the Cretaceous/Paleogene boundary (Martins et al. 2018). In gastropods, species with non-planktotrophic larvae and thus smaller geographic ranges had shorter species durations, but larval types had indistinguishable extinction rates during the end-Cretaceous mass extinction (Jablonski et al. 1997; Jablonski and Hunt 2006).

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Both of these examples demonstrate that rapid changes to the fitness landscape (e.g., during mass extinctions) can disrupt background macroevolutionary trends (Gould 1985), so the relationship between life-history traits and diversification rates can be time varying. In this study, we test the hypothesis that a key life-history trait, brooding, has affected diversification rates in cheilostome bryozoans.

The order Cheilostomatida is a well-supported monophyletic clade of marine bryozoans, which are colonial, suspension-feeding marine invertebrates with calcified skeletons (Waeschenbach et al. 2012). Cheilostomes have a rich 160 Myr fossil record, and they exhibit diverse growth forms and phenotypic, modular polymorphisms that reflect aspects of their ecology. As a result, they have been a study system for research on correlations between ecological traits and macroevolutionary trends (Schopf et al. 1973; Hughes and Jackson 1990; Cheetham et al. 2001). Although cheilostomes first appeared in the fossil record in the Late Jurassic, they underwent a major increase in genus richness during the Cretaceous, at which point they overtook the cyclostome order of bryozoans in diversity and abundance (Jablonski et al. 1997; Sepkoski et al. 2000; Lidgard et al. 2012, 2021; Moharrek et al. 2022). Bryozoan colonies can reproduce sexually through self-fertilization or outcrossing and asexually through fragmentation (O'Dea 2006). The earliest cheilostomes known from the fossil record lack larval brood chambers and bear overall similarity to modern non-brooding species, so it is inferred that they were non-brooding and produced planktotrophic larvae (Taylor 2020). Larval brood chambers first appear in cheilostome fossils from the Albian Stage of the Cretaceous Period (Taylor 1988; Ostrovsky et al. 2008; Fig. 1). Cheilostomes evolved larval brooding independently at least 10 times in multiple lineages (Grant et al. 2023), generating a wide range of convergent incubation structures (Lidgard et al. 2012). Brood chambers can be calcified or membranous and external or internal to the zooid, but calcified, external brood chambers known as ovicells are the most common (Woollacott and Zimmer 1977; Ostrovsky and Taylor 2005; Fig. 1). The energetic cost of brooding varies depending on the degree of calcification and type of matrotrophy (maternal nutrition) (Ostrovsky et al. 2009). Regardless, all brooding strategies are energetically intensive compared with non-brooding, and all brooders produce larvae that are non-planktotrophic and thus have a short larval stage, are larger when they enter the water column, and settle closer to the parent colony than planktotrophic larvae.

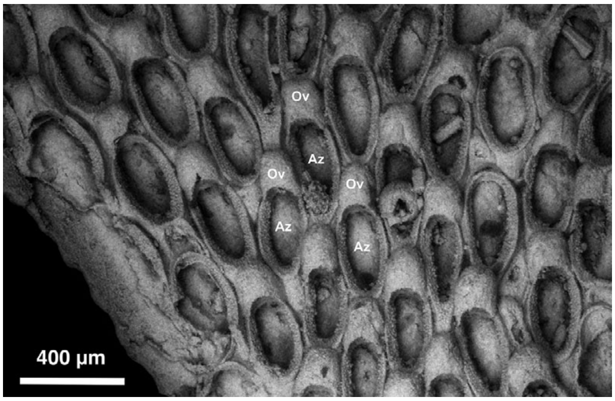

Figure 1. Photo of Cretaceous-age *Wilbertopora listokinae* Cheetham et al., 2006 cheilostome bryozoan colony (USNMPAL 216175), showing autozooids (Az) and external brood structures (ovicells [Ov]).

Taylor (1988) hypothesized that the emergence of larval brooding increased speciation rates in cheilostome lineages and drove their diversification event in the Cretaceous. Because brooded larvae do not typically disperse as far as non-brooded larvae, species that brood their larvae may have lower gene flow between populations and therefore a higher rate of speciation (Taylor 1988; Olsen et al. 2020). Although geographic range size and dispersal distance are not consistently correlated (Lester et al. 2007), genetic recombination between invertebrate populations with non-planktotrophic larvae is indeed low (Crisp 1978; Jackson and Coates 1986; Janson 1987). The rafting of asexually produced colony fragments may keep overall geographic range size high (Worcester 1994), while the low dispersal of brooded larvae may decrease gene flow and increase origination rate (Jablonski and Lutz 1983; Taylor 1988; Watts and Thorpe 2006). The connection between brooding and diversification rate is therefore plausible, and brooders are clearly more diverse than non-brooders today (Fig. 2). However, whether this pattern reflects higher origination rates in brooding cheilostomes or higher extinction rates in non-brooding cheilostomes has not yet been tested using the fossil record. Differences in origination and extinction rates may be time dependent; differential extinction or origination during a particular interval such as the Cretaceous/Paleogene mass extinction may have created the modern diversity gap between brooders and non-brooders. A recent molecular phylogenetic analysis of extant cheilostomes found that brooding and non-brooding lineages have had similar speciation rates (Orr et al. 2022). However, phylogenetic methods rely on extant taxa, making them vulnerable to survivorship bias and obscuring potential time-varying differences in rates (Rabosky 2010; Simpson et al. 2011; Liow et al. 2022; May and Rothfels 2023).

We estimate origination and extinction rates through time for brooding and non-brooding cheilostome genera using the cheilostome fossil record. Based on the hypothesis that reduced gene flow

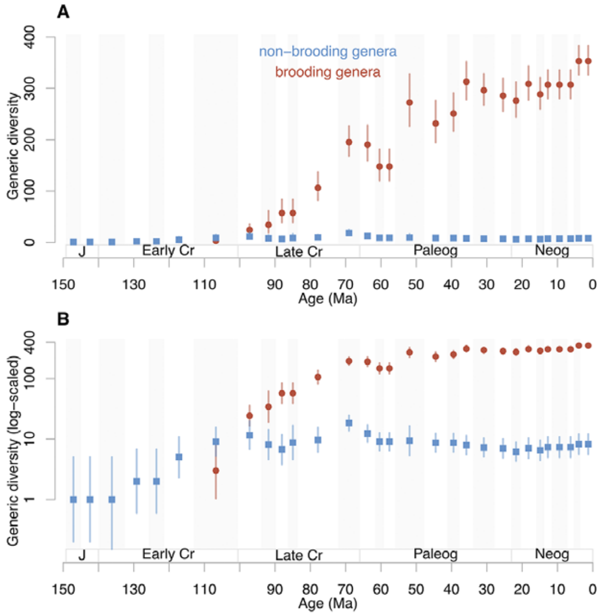

Figure 2. Genus-level diversity of brooding (red circles) and non-brooding (blue squares) cheilostome bryozoans plotted on a **(A)** linear and **(B)** logarithmic axis. Values estimated with capture–mark–recapture (CMR) POPAN model from the Late Jurassic through the Quaternary. Error bars are 95% confidence intervals. Shaded intervals indicate geologic stages.

increases speciation, we predict brooding genera had a higher origination rate. The distinct selective regime of the Cretaceous/Paleogene mass extinction may have disrupted the correlation between brooding and origination, either temporarily or permanently. We use a time-explicit modeling approach that accounts for preservation bias to test whether we can substantiate that the rise of brooding cheilostomes was driven by higher origination rate in brooding lineages, higher extinction rate in non-brooding lineages, or a combination of these two factors.

Methods

Data Compilation

There are two components to our dataset: the record of cheilostome occurrences and the classification of genera into those that brood larvae and those that do not. We use the occurrence data from Lidgard et al. (2021) (both the Age-Only and FosLocal datasets), which have more than 30,000 bryozoan occurrences from the Tithonian to the present with manually vetted ages and updated taxonomic assignments, as well as the recent monograph by Håkansson et al. (2024). We omit occurrences whose ages are not constrained to a single one of our time bins (see description of time bins later). We conduct our analysis at the genus level instead of the species level to mitigate the effects of fossil preservation and sampling on known taxon ages (Forey et al. 2004). While genus-level analysis can be problematic when investigating traits that vary within genera (Hendricks et al. 2014), larval development mode is largely conserved within families.

Historically, non-brooding cheilostome families were categorized into the suborder Malacostegina, which has been synonymized with the suborder Membraniporina (Cook et al. 2018). There are currently six families assigned to Membraniporina in the World Register of Marine Species (Ahyong et al. 2024): Chiplonkarinidae, Corynostylidae, Electridae, Membraniporidae, Sinoflustridae, and Wawaliidae. We classify all of their genera as non-brooders. From a manual literature search (included in our Supplementary Files), we find there are 70 cheilostome genera in brooding families for which brood chambers have not been described. Of these 70 genera, we infer 57 are brooders, because they are in predominantly brooding families, brood chambers are not always preserved in fossils, and brooding has never been known to be lost in a lineage once it has evolved (Orr et al. 2022). We omit the other 13 ambiguous genera (only 47 occurrences) from our study, because they are from rare, unusual, or understudied families that make them difficult to classify (see list in Supplement). In our main analyses, we thus have 630 brooding genera with 13,927 total occurrences and 32 non-brooding genera with 899 total occurrences. In the Supplement, we also include a sensitivity analysis, in which we reclassify all 57 genera of inferred brooders as non-brooders to show that even in the implausible scenario that all of these genera are in fact non-brooders, our best-fitting extinction and origination model results do not change.

Estimating Diversity, Origination, and Extinction Rates

We choose a method of estimating diversity, origination, and extinction rates based on the attributes of our dataset. Our sample size of brooding genera is larger than that of non-brooding genera, but this sample size difference reflects genuine differences in diversity. There are 7 non-brooding genera with only 1 occurrence, and 127 brooding genera with only 1 occurrence. Furthermore, to estimate diversity, origination, and extinction rates, we must also fit a sampling rate model, because fossil preservation and sampling effort are never complete and vary through time. Therefore, we choose to fit Pradel seniority capture–mark–recapture (henceforth CMR, although there are alternative CMR family models) models, which use full occurrence histories to estimate sampling probability, survival probability, and recruitment probability (Pradel 1996; Liow and Nichols 2010). Sampling, survival, and recruitment probabilities are then converted to sampling, extinction, and origination rates per time bin. Because our time bins are of different lengths, we divide our rates by the duration of each time bin, yielding rates in units of genera per million years. We also use a POPAN CMR model to estimate genus-level diversity through time while accounting for estimated sampling rate (Franeck and Liow 2019). Exact CMR implementation varies across the paleontological literature (Liow et al. 2015; Martins et al. 2018; Sibert et al. 2018; Franeck and Liow 2019), so we further explain our approach in the Supplement.

We compare CMR models by corrected Akaike information criterion (AICc) score to determine which covariates explain the most variation in the data (Hu 2007). AICc scores are penalized for the number of model parameters and adjusted for small sample sizes, both of which should prevent overfitting. For origination and extinction rates, we fit models with only time bin, only brooding, and then an interaction between time bin and brooding as the covariates, as well as a null model with no covariate. For sampling rate, we fit models with only time bin as the covariate and with an interaction between time bin and brooding as the covariates. We do not include a brooding-only model for sampling rate, because we do not have a reasonable hypothesis for why brooders and non-brooders would be sampled differently throughout the entire time series. In total we compare 24 models. We use the RMark R package (Laake 2013), which interfaces with the independent MARK software (White and Cooch 2001) to fit our models. CMR has the advantages of not assuming a constant sampling rate and being able to include singleton genera (Nichols and Pollock 1983; Liow and Nichols 2010). For the sake of comparison, we also estimate classic boundary-crosser, per capita origination and extinction rates (Foote 2000a,b). We include the per capita model results in the Supplement to show that the method chosen does not meaningfully affect our results (Supplementary Fig. 1).

For time bins, we use ordered geologic stages from the Tithonian to the present, except we pool the Zanclean and Piacenzian into one Pliocene time bin and we pool all the Pleistocene and Holocene stages into one Quaternary time bin to reduce variance in interval duration. These are the time intervals between which the CMR models calculate sampling, origination, and extinction probabilities. However, there are not enough non-brooding genera to fit well-constrained stage-level models (Supplementary Fig. 2). Instead, we use larger time bins as our time covariate: pre-cheilostome radiation (Tithonian–Albian), the cheilostome radiation (Cenomanian–Campanian), the end-Cretaceous mass extinction and recovery (Maastrichtian–Thanetian), the Eocene and Oligocene (Ypresian–Chattian), and the Neogene and Quaternary (Aquitanian–Holocene). We use ordered categorical time bins rather than a single continuous time parameter. If we made time a continuous variable, we would be fitting a linear model with one origination and one extinction estimate for the entire time series, which would not allow us to test for time-varying differences in rates (Martins et al. 2018; Sibert et al. 2018; Franeck and Liow 2019).

We choose these longer time bins as our time covariate to highlight what we suspect are distinct phases of cheilostome macroevolution (Lidgard et al. 2021; Moharrek at al. 2022).

Results

In our best-fitting model, origination rate is a function of an interaction between brooding and time bin, while extinction rate is only a function of time bin (Table 1, Fig. 3). The ΔAICc of this model relative to the second-best model is greater than 5, exceeding the conventional cutoff of ΔAICc = 2 for a meaningful difference between model fit (Burnham and Anderson 2002). Our analysis therefore suggests that brooding has a time-varying effect on origination rate, but brooding has no effect on extinction rate. The first known brooding genus appears in the Albian, and the origination rate of brooders is significantly higher than that of non-brooders in the Cenomanian–Campanian (brooders = 0.106 ± 0.024/Myr, non-brooders = 0.047 ± 0.035/Myr). Origination rates for both groups then decrease and converge toward the present. Because this pattern is potentially consistent with diversity-dependent origination rates (Jablonski et al. 1997; Foote 2023), we compared our best-fit model to a model in which origination rate is simply a function of genus richness. The brooding-time model is strongly preferred over the genus richness model (ΔAICc = 52.9), so diversity-dependence alone cannot explain this trend in cheilostome origination (see Supplement). Non-brooders have a high origination rate in the Tithonian–Albian (0.084 ± 0.055/Myr), but once brooding evolves, the non-brooder origination rate remains equal or lower than brooding origination rates to the present. The overall cheilostome extinction rate is significantly higher in the Maastrichtian–Paleocene due to the end-Cretaceous mass extinction (0.066 ± 0.011/Myr), consistent with previous work (McKinney and Taylor 2001; Lidgard et al. 2021; Moharrek et al. 2022). However, brooders and non-brooders do not have distinct extinction rates in any interval.

While the best model illustrates which factors explain the most variation, the full suite of models provides additional information. In the model that does not allow origination rates to vary through time, we cannot detect a difference in origination rates between brooding and non-brooding genera (Fig. 4). The model in which extinction and origination are a function of brooding without time covariance is ranked 21st out of the 24 models (ΔAICc = 378). We also fit a stage-level model to show overall trends in cheilostome origination and extinction rates through time (Supplementary Fig. 2). There are not enough non-brooding genera for a stage-level model to estimate distinct rates for brooders and non-brooders.

The Cenomanian–Campanian is the key interval when brooders had a higher origination rate than non-brooders. To estimate how different origination rates were in this interval compared with all other intervals, we ran a post hoc model in which the time bins were reduced to Tithonian–Albian, Cenomanian–Campanian, and Maastrichtian–Quaternary (Supplementary Fig. 3). We still find brooders have a higher origination rate than non-brooders in the Cenomanian–Campanian, but we also note that all cheilostomes have higher origination rates in this interval than throughout the Maastrichtian–Quaternary.

Table 1. Corrected Akaike information criterion (AICc) comparison for capture–mark–recapture (CMR) models. Model 1 is plotted in Fig. 3 and model 21 is plotted in Fig. 4. The covariate time_bin refers to five time intervals: Tithonian–Albian, Cenomanian–Campanian, Maastrichtian–Thanetian, Ypresian–Chattian, and Aquitanian–Holocene.

Rank	Extinction	Sampling	Origination	ΔAICc
1	~time_bin	~brooding * time_bin	~brooding * time_bin	0
2	~time_bin	~brooding * time_bin	~time_bin	30.4
3	~time_bin	~time_bin	~time_bin	66.6
4	~brooding * time_bin	~brooding * time_bin	~time_bin	71.1
5	~brooding * time_bin	~brooding * time_bin	~brooding * time_bin	74.0
6	~time_bin	~time_bin	~brooding * time_bin	89.2
7	~brooding * time_bin	~time_bin	~brooding * time_bin	103.5
8	~brooding * time_bin	~time_bin	~time_bin	108.7
9	~brooding * time_bin	~brooding * time_bin	~brooding	182.1
10	~time_bin	~brooding * time_bin	~brooding	189.8
11	~1	~brooding * time_bin	~brooding * time_bin	219.2
12	~1	~time_bin	~brooding * time_bin	219.7
13	~brooding	~brooding * time_bin	~brooding * time_bin	220.0
14	~brooding	~time_bin	~brooding * time_bin	220.9
15	~brooding	~brooding * time_bin	~time_bin	239.7
16	~1	~brooding * time_bin	~time_bin	256.2
17	~brooding	~time_bin	~time_bin	268.3
18	~time_bin	~time_bin	~brooding	269.1
19	~brooding * time_bin	~time_bin	~brooding	274.1
20	~1	~time_bin	~time_bin	287.6
21	~brooding	~brooding * time_bin	~brooding	378.4
22	~1	~brooding * time_bin	~brooding	381.1
23	~1	~time_bin	~brooding	474.4
24	~brooding	~time_bin	~brooding	475.8

Discussion

We find the emergence of larval brooding is correlated with the origination rate but not the extinction rate of cheilostome bryozoans. (Fig. 3B,C). During the Cenomanian–Campanian, brooding genera had a significantly higher origination rate than non-brooding genera. This spike in origination rate supports Taylor's (1988) hypothesis that brooding is associated with increased origination rate and corresponds to the timing of the end-Cretaceous cheilostome diversification (Moharrek et al. 2022). During this diversification event, the cheilostome order became more abundant and diverse than the cyclostome order and remains so to the present

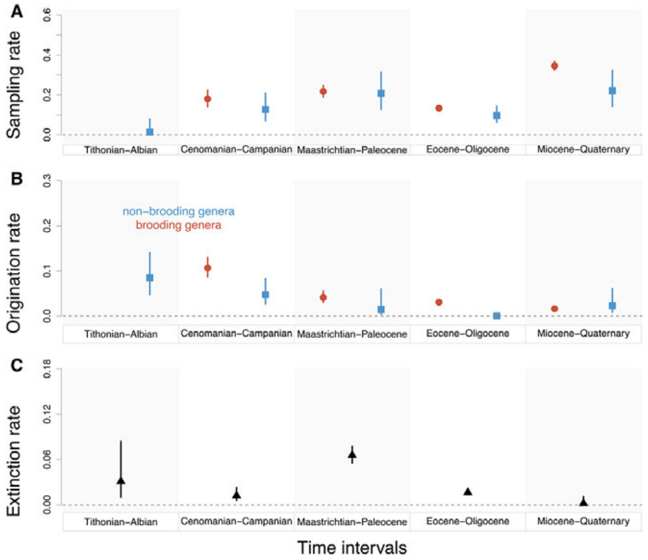

Figure 3. Pradel seniority capture–mark–recapture (CMR) results of our best-fitting model (model 1 in Table 1). **A,** Sampling rates differ for brooding (red circles) and non-brooding (blue squares) genera across time intervals. **B,** Origination rates differ over time and across brooding and non-brooding genera. **C,** Extinction rates (black triangles) for brooding and non-brooding genera are not significantly different from each other, but extinction rate varies across time intervals. Brooding genera are not plotted in the Tithonian–Albian interval, because they first appear in the fossil record in the Albian. Error bars are 95% confidence intervals. Rates are genera per million years.

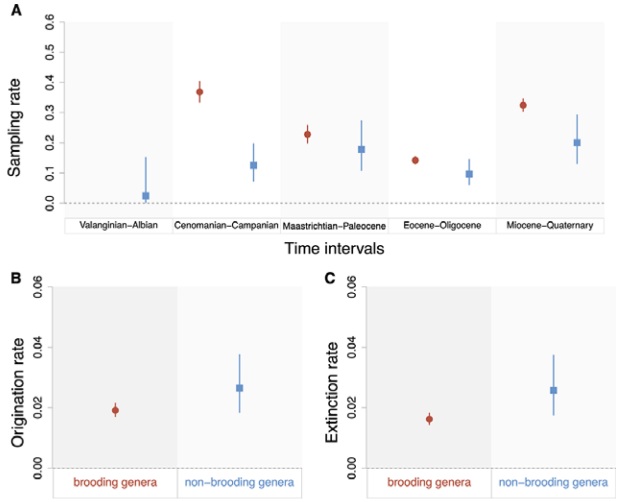

Figure 4. Pradel seniority capture–mark–recapture (CMR) results of the brooding-only model (origination and extinction not time-varying; model 21 in Table 1). **A,** Sampling rate is similar to the results presented in Fig. 3A. **B,** Origination rate and **(C)** extinction rate are not appreciably different between brooding (red circle) and non-brooding (blue square) genera when temporal variation is not considered. Brooding genera are not plotted in the Valanginian–Albian interval, because they first appear in the fossil record in the Albian. Error bars represent 95% confidence intervals. Rates are genera per million years.

(Sepkoski et al. 2000; Lidgard et al. 2021). Our results suggest that brooding played a role in this shift in bryozoan clade dominance, as brooding genera diversify during the key interval in which cheilostomes overtook cyclostomes in diversity. Interestingly, cyclostomes independently evolved a distinct form of larval brooding, which did not lead to a radiation as pronounced as the cheilostome radiation (Taylor and Larwood 1990). It has not been adequately explained how brooding would cause an origination event in cheilostomes but not cyclostomes (Moharrek et al. 2022). Our study provides additional insight into this larger body of questions about turnover between bryozoan clades.

The decreasing difference in origination rates between brooders and non-brooders over time is unexpected. We hypothesized that the end-Cretaceous mass extinction may have created a selective regime that nullified or reversed the background relationship between brooding behavior and macroevolution, as observed in past studies of other taxa (Jablonski et al. 1997; Martins et al. 2018). Instead, the decrease in the effect of brooding is gradual, not specific to the extinction–recovery interval. We also cannot explain the decrease as a consequence of diversity-dependent origination. Non-brooders have their highest origination rates in the Tithonian–Albian before brooders are prevalent, and then their origination rate drops as brooders diversify. Whether trait novelty drove an early burst for brooders at the expense of non-brooders or environmental conditions in the Cenomanian–Campanian simply favored brooders over non-brooders is worth further investigation.

Our results have varied degrees of support for previous studies of cheilostome diversification. Our extinction and origination rate estimates are broadly consistent with the results of Lidgard et al. (2021) and Moharrek et al. (2022), despite differences in rate estimation methods. Our results differ from those of Orr et al. (2022), who did not find different speciation rates between brooding and non-brooding cheilostomes in their main analyses. However, with an alternate basal tree topology, they did find an unknown trait associated with brooding increases speciation rate. Orr et al. (2022) conducted their analyses at the species level and had fewer non-brooders in their dataset than we do, which may have lowered the statistical power of their tests. In addition, cheilostome origination rates have become more similar toward the present, making it difficult to detect rate differentials of past time intervals. Our use of time-varying models improved our ability to distinguish the macroevolutionary rates of brooders and non-brooders. The temporal variation in the influence of brooding on origination rate may explain why phylogenetic approaches have failed to detect different origination rates between brooding and non-brooding cheilostomes.

Larval brooding in cheilostomes is correlated with other colony traits besides dispersal, which could affect origination rates through alternative mechanisms. Larval brooding evolved convergently in at least 10 different lineages of cheilostomes, and brooders and non-brooders are not monophyletic groups (Grant et al. 2023). Therefore, phylogenetic relatedness is unlikely to be a confounding factor in the relationship between brooding and origination rate. However, brooding genera also have more polymorphs and greater colony complexity than non-brooding genera (Simpson 2021). Complexity is correlated with other colony traits such as metabolic rate, growth rate, life span, fecundity, and overgrowth success for encrusting cheilostomes (Strathmann and Strathmann 1982; Strathmann 1985; Sepkoski et al. 2000; Liow et al. 2019). While our results are consistent with Taylor's hypothesis, brooders' high initial origination rate may be underpinned by these covarying and potentially confounding traits.

Alternatively, the high early origination rate of brooding genera may have aided the proliferation of traits affiliated with brooding. If so, we would expect cheilostome genera with lower fecundity, other types of polymorphic zooids (avicularia), and higher metabolic rates to also have higher origination rates in the Cenomanian–

Campanian. This is an interesting set of testable predictions, and it is also worth investigating whether this suite of life-history traits are correlated through time or decouple at any point due to diverging selective pressures. To verify that brooding could have increased origination specifically by reducing gene flow, future work should measure species richness and gene flow in co-occurring brooding and non-brooding genera. Furthermore, the dispersal distance of larvae, both planktotrophic and non-planktotrophic, varies substantially with latitude (Álvarez-Noriega et al. 2020), and non-planktotrophic larvae have dispersal distances that vary with larval body size (Marshall and Keough 2003). Another interesting avenue for future research is whether bryozoan origination rates vary with larval body size and latitude.

Like Bryozoa, the Annelida, Arthropoda, Echinodermata, Mollusca, Porifera, and possibly Paleozoic Brachiopoda all contain clades with both brooding and non-brooding reproductive modes (Jablonski and Lutz 1983; Emlet 1985; McEdward and Janies 1997; Whalan et al. 2005; Rouse and Pleijel 2006; Watling and Thiel 2013). In the Recent, brooding is correlated with population attributes related to speciation across these groups. Brooding is known to decrease dispersal in modern gastropods and corals (Jablonski et al. 1997; Nishikawa et al. 2003) and increase genetic differentiation between populations in modern corals and echinoderms (Hellberg 1996; Sponer and Roy 2002; Nishikawa et al. 2003). Brooding is correlated with species duration in gastropods (Hansen 1980) and bivalves (Kauffman 1975). While not all these taxa have a fossil record substantial enough to test whether larval brooding's effect on these population attributes has increased their speciation rates, aspects of this mechanism are thus supported across several phyla. Substantiating the link between population attributes observable on short timescales and trends on macroevolutionary timescales requires integrating modern ecological and paleontological research, an exciting forefront of collaboration.

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Competing Interests. The authors have no conflicts of interest to report.

Data Availability Statement. All data used in the analyses are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1vhhmgr44. Supplementary Files uploaded to Zenodo: 10.5281/zenodo.14104270.

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